

Dispersal of tropical fishes to temperate seas in the southern hemisphere

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Abstract

Western boundary currents in the Southern Hemisphere are capable of dispersing tropical fishes to temperate areas by carrying eggs and larvae from northern breeding grounds in a southerly direction. However, most eastern boundary currents prevent such a dispersal by flowing in the reverse direction, *i.e.* northwards. An exception to this is the Leeuwin Current, an eastern boundary current which flows southwards along the Western Australian coastline. Furthermore, unlike other south-flowing currents which disperse tropical fishes predominantly during the summer, the Leeuwin Current is involved in an autumn and winter dispersal. This unusual pattern was examined by investigating the temporal and spatial aspects of tropical reef fish recruitment at Rottnest Island (latitude 32°S) in south-western Australia. In addition, this pattern was compared with available data on tropical fish recruitment in other temperate areas of the Southern Hemisphere.

Introduction

The dispersal of tropical marine animals by ocean currents to areas outside their normal breeding ranges is well known, the best documented example involving the Gulf Stream, a western boundary current flowing polewards in the North Atlantic (Randall 1968, Briggs 1974, Thresher 1985). Propagules of animals inhabiting the Caribbean region are picked up by the current and carried northwards along the North American east coast. During the summer, many tropical species are found in sheltered bays in temperate areas, only to disappear with the onset of colder conditions in winter. In the Southern Hemisphere, western boundary currents flowing polewards off South Africa, Australia, and South America, also transport eggs and larvae from tropical breeding grounds southwards to temperate areas during the summer months (Smith 1949, Briggs 1974, Thresher 1985). By contrast, the eastern boundary currents that flow towards the equator in the Southern Hemisphere generally prevent dispersal of tropical forms to temperate areas by flowing in the reverse direction. The exception to this is the Leeuwin Current off south-western Australia, a southward-flowing current originating in waters off north-western Australia (Pearce 1991). This body of warm water provides a vehicle for tropical animals to disperse along the south-western coastline. However, unlike most other poleward-flowing currents, it flows predominantly during the autumn and winter months. During the summer, a northerly flow of cooler water - the West Australian Current - is thought to be the dominant pattern (Maxwell & Cresswell 1981).

For this study, the unusual pattern of a southward-flowing eastern boundary current dispersing tropical species to temperate coasts during the colder months was examined. The investigation was mainly centred

on a study of the recruitment of tropical reef fishes at Rottnest Island, Western Australia (latitude 32°S), during the period 1979-1985. As well as examining the spatial and temporal aspects of this recruitment, the degree of persistence of the fauna was also considered. To contrast this situation, information was gathered on, firstly, the summer recruitment of tropical fishes by western boundary currents, in particular the East Australian Current, and secondly, the lack of dispersal of tropical species by the eastern boundary currents off the south-western coasts of Africa and South America.

Leeuwin Current

The occurrence of tropical animals in the littoral fauna of south-western Australia has been known since the early investigations of Saville-Kent (1897) and Michaelsen (1908). Subsequent authors (eg Hodgkin & Marsh 1957) suggested that this was related to the presence of a warm, south-flowing current, now known as the Leeuwin Current (Cresswell & Golding 1980). The characteristics of this current are dealt with elsewhere in this publication, but for the purposes of this paper, brief mention of some of its features is necessary. The Leeuwin Current is a stream of warm, low salinity water flowing southwards over the continental shelf in the region of North West Cape (22°S) and Shark Bay (26°S), but moving off the shelf at about 27°S and passing to the west of the Houtman Abrolhos (29°S) and Rottnest Island (32°S). It then rounds Cape Leeuwin (34°S), and flows eastwards across the Great Australian Bight. Satellite imagery and satellite-tracked buoys indicate that the current flows predominantly in autumn and winter, and can reach speeds of between two and three knots (about 80 to 120 kilometres per day) (Pearce 1989).

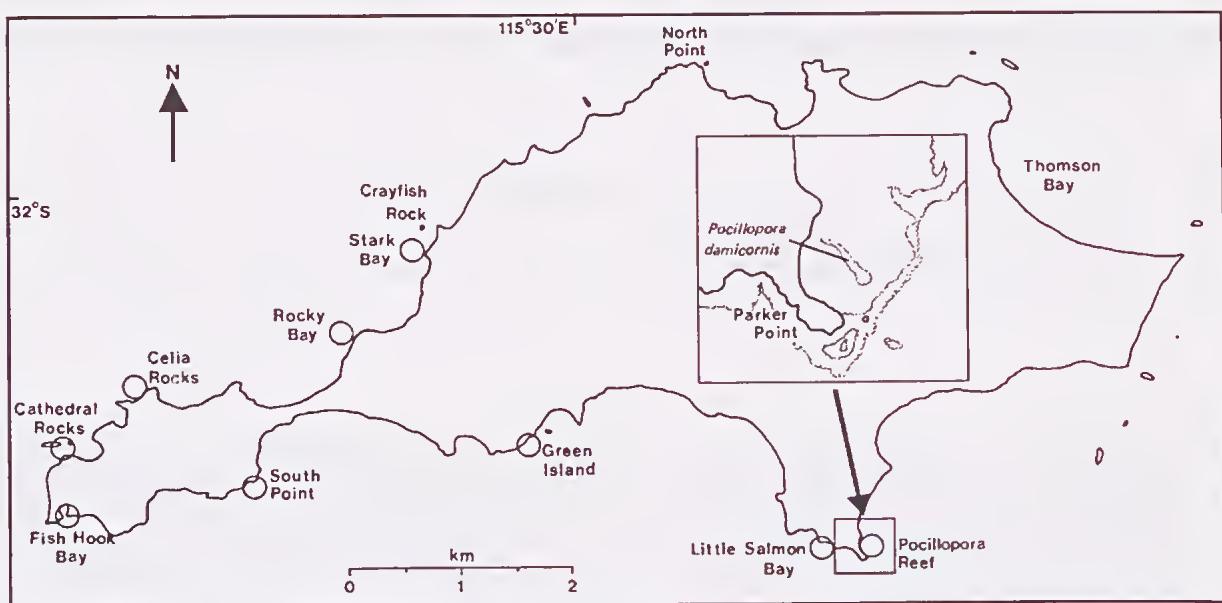


Figure 1 Map of Rottnest Island showing areas of tropical reef fish concentrations (circles). Insert shows an enlargement of the Pocillopora Reef area.

The apparent role played by the Leeuwin Current in the dispersal of tropical fishes along the south-western coastline has been commented on by several authors (Hutchins 1977 & 1979, Maxwell & Cresswell 1981, and Wilson & Allen 1987). There seems little doubt that it is the major contributor to the large size of the transition zone between the temperate and tropical faunas, which ranges from approximately 23° to 35°S. However, the reduction in the numbers of tropical species as latitude increases is more punctuated than gradual. Rottnest Island, at 32°S, is near the southern limit of this transition zone, but nevertheless possesses an unusually rich tropical reef fish fauna. Reefs along the adjacent mainland coast are, by comparison, almost devoid of tropical species. Indeed, the closest inshore reefs to Rottnest Island which enjoy a similar tropical richness are 200 km to the north in the vicinity of Jurien Bay (30°18'S). Is there a connection between Rottnest Island and the Leeuwin Current which may account for this faunal difference?

Rottnest Island is located 18 km off the Western Australian coast, lying close to the edge of the continental shelf. The western portion of the island is bathed by peripheral waters of the Leeuwin Current during autumn and winter (Cresswell & Golding 1980), a feature reflected in the considerably higher minimum water temperatures at the island than in adjacent mainland waters (Hodgkin & Marsh 1957, Hodgkin & Phillips 1969). During the present study, water temperatures taken along the western portion of the island were rarely below 18°C, whereas in mainland coastal waters, the mean minimum was 15°C. The seas of the island are home to a diverse array of fishes best described as belonging to a warm-temperate fauna. However, prominent numbers of tropical species also occur. Of the 360 fishes recorded for the inshore waters of the island, 98 or 27% are tropical species. Of the

latter number, 61 species (Table 1) are considered to be either reef dependent or associated with this habitat. In contrast only 11 species of tropical reef fishes have been found in the nearby mainland waters of Perth.

The tropical reef fish fauna of Rottnest Island is concentrated in shallow bays along the western two-thirds of its coastline (Fig. 1); one of these areas is particularly noteworthy. Pocillopora Reef is a shallow lagoon, protected by a prominent headland and a system of seaward reef crests. Its special feature is a 100 m long reef consisting mostly of the coral *Pocillopora damicornis* (see insert, Figure 1). Other smaller colonies of this coral are scattered throughout the lagoon, as well as species of at least five additional coral genera. Reef-dwelling fishes are commonly found in the vicinity of this reef, with smaller numbers in other parts of the lagoon. Large adults of certain species are always present, particularly labrids of the genus *Thalassoma*, but other species have been recorded on the basis of juveniles only. In contrast, the more exposed reefs outside the lagoon support few tropical species, and, in most respects, are generally typical of other temperate reefs in south-western Australia. Nevertheless, some of the deeper reefs around the island are occasionally inhabited by particular tropical fishes which are, at least as adults, rarely seen in these shallow bays.

During autumn, an influx of very small juveniles of tropical fishes occurs on the reefs along the western portion of the island. In the lagoon at Pocillopora Reef, the largest numbers settle either in the shallows at the base of the headland, or in the reef of *Pocillopora damicornis*. This recruitment continues spasmodically throughout the winter, normally ceasing in November (Table 2). In some years, a temporary increase in the numbers settling may occur in October. However, during the period of this investigation, the young of only

Table 1
Tropical reef fishes recorded for south-western Australia

(1 = Rottnest Island; 2 = Perth; 3 = Geographe Bay; 4 = Cape Naturaliste; 5 = Albany; 6 = Recherche Archipelago; j = juvenile; a = adult).

Species	1	2	3	4	5	6
<i>Plotosus lineatus</i>	j,a					j
<i>Antennarius nummifer</i>	j					
<i>Pterois volitans</i>	j,a	a				
<i>Psammoperca waigiensis</i>	a	a				
<i>Epinephelus lanceolatus</i>	a					
<i>Epinephelus rivulatus</i>	a					
<i>Belonepterygion fasciolatum</i>	j					
<i>Plectorhinchus flavomaculatus</i>	a		a			
<i>Plectorhinchus schotaf</i>	a					
<i>Parupeneus chrysopleuron</i>	j,a					
<i>Parupeneus signatus</i>	j,a	j				
<i>Pempheris ovalensis</i>	j,a					
<i>Pempheris schwenkii</i>	j					
<i>Platax teira</i>	j,a	j	a		a	
<i>Chaetodon auriga</i>	j,a					
<i>Chaetodon citrinellus</i>	j					
<i>Chaetodon lineolatus</i>	a					
<i>Chaetodon lunula</i>	j,a					
<i>Chaetodon plebeius</i>	j,a					
<i>Abudefduf sexfasciatus</i>	j,a					
<i>Abudefduf sordidus</i>	j					
<i>Abudefduf vaigiensis</i>	j,a					
<i>Plectroglyphidodon leucoxanthus</i>	j,a					
<i>Pomacentrus coelestis</i>	j					
<i>Pomacentrus milleri</i>	j,a					
<i>Stegastes obreptus</i>	j,a					
<i>Anampsese caeruleopunctatus</i>	j					
<i>Anampsese geographicus</i>	j,a				a	
<i>Cheilio inermis</i>			a			
<i>Coris aygula</i>	j,a					
<i>Gomphosus varius</i>	j,a					
<i>Hemigymnus faciatus</i>	j					
<i>Labroides dimidiatus</i>	j,a					
<i>Stethojulis bandanensis</i>	j,a					
<i>Stethojulis strigiventer</i>	j,a					
<i>Thalassoma amblycephalum</i>	j					
<i>Thalassoma hardwicke</i>	j					
<i>Thalassoma lunare</i>	j,a					
<i>Thalassoma lutescens</i>	j,a					
<i>Thalassoma purpureum</i>	j,a					
<i>Scarus festivus</i>	a					
<i>Scarus ghobban</i>	j,a					
<i>Scarus gibbus</i>	j					
<i>Scarus reticulatus</i>	j					
<i>Scarus schlegeli</i>	j,a					
<i>Scarus sordidus</i>	j,a					
<i>Entomacrodus striatus</i>	j					
<i>Omobranchus germaini</i>	j,a	j,a				
<i>Petroscirtes breviceps</i>	j	j,a				
<i>Petroscirtes mitratus</i>	j	j,a				
<i>Plagiotremus rhinorhynchos</i>	j,a			a		
<i>Plagiotremus tapeinosoma</i>	j,a				a	
<i>Norfolkia brachylepis</i>	j,a					
<i>Amblygobius phalaena</i>	a					
<i>Barbuligobius bohlkei</i>						j
<i>Gnatholepis inconsequens</i>	a					
<i>Priolepis nuchifasciatus</i>			a			
<i>Ptereleotris evides</i>	j					
<i>Acanthurus nigrofasciatus</i>	j					
<i>Acanthurus triostegus</i>	j					
<i>Naso unicornis</i>	j					
<i>Siganus fuscescens</i>	j					
<i>Balistoides viridescens</i>	a		a			
<i>Ostacion cubicus</i>			j			
<i>Arothron hispidus</i>			j			
<i>Diodon holacanthus</i>			j			

Table 2
Summary of times of recruitment of 23 species of tropical reef fishes at Rottnest Island

Species	J	F	M	A	M	J	J	A	S	O	N	D
<i>Plotosus lineatus</i>			X									
<i>Parupeneus chrysopleuron</i>					X							
<i>Parupeneus signatus</i>			X									
<i>Pempheris ovalensis</i>			X			X	X					
<i>Chaetodon plebeius</i>												X
<i>Abudefduf sexfasciatus</i>	X		X		X							
<i>Abudefduf vaigiensis</i>	X		X		X							X
<i>Plectroglyphidodon leucozonus</i>			X									
<i>Stegastes obreptus</i>				X		X						
<i>Arampus geographicus</i>					X	X	X	X				X
<i>Labroides dimidiatus</i>			X									
<i>Stethojulis bandanensis</i>						X			X			X
<i>Stethojulis strigiventer</i>				X								
<i>Thalassoma lunare</i>								X	X			X
<i>Thalassoma lutescens</i>			X					X				X
<i>Thalassoma purpureum</i>			X			X	X	X				X
<i>Scarus ghobban</i>					X				X			
<i>Scarus gibbus</i>								X				
<i>Ptereleotris evides</i>						X						
<i>Omobranchus germaini</i>	X	X										
<i>Acanthurus nigrofasciatus</i>					X							
<i>Acanthurus triostegus</i>			X	X		X						X
<i>Naso unicornis</i>						X						

one species, the blenny *Omobranchus germaini*, were recruited during the summer months.

The times of settlement for some species were difficult to determine. Although species such as the pomacentrids *Abudefduf vaigiensis* and *A. sexfasciatus* remain in the open after settling, others such as the labrids *Thalassoma purpureum* and *T. lutescens* hide among the rocks and coral and are therefore difficult to detect. Thus, the times of recruitment for some species, as indicated in Table 2, may be affected by this cryptic phase.

Many of the small tropical fish which settle at the Island disappear during the subsequent months, perhaps falling prey to predators, or even succumbing to unfavourable environmental conditions. However, some of the hardier species persist right through the winter months, often surviving to adulthood. These either remain in the shallow bays or move out to deeper offshore reefs as they become larger.

In contrast to the above pattern of recruitment, Russell *et al.* (1977), working on the tropical reef fish fauna at Queensland's One Tree Island (latitude 23°30'S), showed that a peak in recruitment occurs in summer, with most species having a breeding season in the mid spring to early autumn period. They found no evidence of settlement during June and July. This summer peak in recruitment also appears to occur on the coral reefs of Western Australia's northern waters (G R Allen, pers comm). Why is there a difference at Rottnest Island?

As noted earlier, the Leeuwin Current flows predominantly during autumn and winter, weakening and moving away from the island in summer. This

close relationship between the commencement and subsequent cessation of tropical recruitment at the island and the arrival and departure of the Leeuwin Current indicates that this current is obviously carrying the young of these tropical fish species to Rottnest Island. The two peaks of recruitment possibly involve larvae from the end of one northern breeding season (late summer - early autumn) and the beginning of the next (mid spring). (Evidence provided by satellite imagery does show that in some years the Leeuwin Current is still present in the Rottnest Island area during October). Individuals recruited during the winter months may include late arrivals at the island which have been temporarily trapped in isolated eddies of the current. Furthermore, the lack of new recruits in summer suggests that tropical reef fishes are not breeding at Rottnest Island. As mentioned earlier, the only exception to this is the blenny *Omobranchus germaini*, a hardy inhabitant of shallow reef flats and intertidal areas which is able to tolerate a considerable range of environmental conditions. It is widespread at the island and is also one of the few tropical reef fishes which is reasonably numerous on the coastal reefs of the nearby mainland.

The most likely source of breeding stocks to the north of Rottnest Island is the Houtman Abrolhos, an area also in the path of the Leeuwin Current. Although a considerable distance south of the tropics, many of the tropical reef fishes at the Houtman Abrolhos appear to be breeding successfully (G R Allen, pers comm); this includes most of those tropical species recorded for Rottnest Island. The latter all have pelagic larvae which are capable of surviving in the plankton for moderate periods (eg larval durations of between 39 and 55 days for *Thalassoma lunare* and 19 to 27 days for *Abudefduf vaigiensis* are given by Victor 1986 and

Thresher *et al.* 1989, respectively). This should easily be enough time for the planktonic larvae to cover the 350 km between the Houtman Abrolhos and Rottnest Island at a current rate as high as 2-3 knots, even allowing for breaks in southwards movement due to meanders and eddy formation, etc.

South of Rottnest Island, records of tropical reef fishes are spasmodic and widespread (Table 1), with two species being found as far east as the Recherche Archipelago. The report of *Epinephelus lanceolatus* from the Coorong in south-eastern South Australia by Kailola & Jones (1981) indicates the great distances that can be covered by current-borne tropical larvae. Nevertheless recruitment success for tropical reef fishes in these more southern areas appears to be poor.

Therefore, the connection between Rottnest Island and the tropical richness of its fauna is primarily the offshore location of the island and the influence of the Leeuwin Current. This current flows well offshore from mainland reefs and other inshore islands, but bathes the western portion of Rottnest Island. Not only does the current carry the propagules of tropical reef fishes to the island, but it also maintains relatively high water temperatures during the winter. In addition, Rottnest Island provides numerous protected habitats which are conducive to settlement by tropical larvae. The corals in these areas obviously provide the shelter and food preferred by them. Some tropical species probably reach mainland reefs in the wind-blown upper surface layers of the water column, but only the very hardiest of species survive the less favourable inshore conditions.

East Australian Current

The presence of significant numbers of tropical reef fishes in south-eastern Australia during summer has long been an attraction for recreational divers and aquarists (Lawler 1984, Fallu 1985). Although a relatively rich tropical fauna occurs all year round on the reefs of northern New South Wales (approx. 30°S), this fauna gradually diminishes as the latitude increases, becoming more of a seasonal phenomenon in central New South Wales (approx. 33°S), and eventually disappearing in the region of the Victorian border (latitude 37°30'S). Nevertheless some localities near the southern extremity of this range possess prominent numbers of tropical fishes during the summer months. An unpublished report (Kuiter 1981) on the fishes of Montague Island (36°15'S) listed 75 species of tropical reef fishes, and a survey by the present author in 1981 at the nearby mainland locality of Merimbula (37°S) produced 50 species. The latter investigation involved a study of the recruitment of tropical reef fishes near the entrance to Merimbula Lake. Here, the recruitment of tropical fishes commences in late November or early December, and continues until about April. These times coincide with the southwards movement of the East Australian Current, which brings warmer tropical waters down the eastern Australian coast to Bass Strait, mainly in summer (Rochford 1984). In autumn the current moves

away from the coast and tropical recruitment ceases. With the onset of unfavourable environmental conditions in winter, most individuals of these tropical species disappear during May and June. At Montague Island, however, a few of the hardier species (eg the scorpaenid *Pterois volitans*) may persist throughout the winter, especially when water temperatures remain higher than normal (Kuiter 1981).

Comparing the dispersal of tropical reef fishes between south-eastern and south-western Australia, temporal and spatial differences are obvious. In south-eastern Australia, recruitment takes place mostly during the summer months, with significant numbers of recruits being found as far south as latitude 37°S, whereas in south-western Australia, recruitment is more of a late autumn to winter phenomenon and virtually ceases at latitude 32°S. This can be best explained by the seasonal differences in flow of the respective currents. The summer-flowing East Australian Current transports its larvae southwards during a period of rising water temperatures, so settlement occurs when conditions are more favourable. In contrast, the Leeuwin Current transports larvae during times when water temperatures are falling, and therefore, only the hardiest are likely to survive. In addition, more propagules of tropical fishes - which generally breed during the warmer months - would be available to a summer-flowing current than a winter-flowing one.

Southern Africa

The Agulhas Current transports propagules of tropical reef fishes to temperate areas of South Africa in summer (Penrith 1976, Beckley 1985). This dispersal occurs regularly to Algoa Bay (34°S) but occasionally such transients are found in the vicinity of the Cape of Good Hope (Beckley *et al.* 1987). Generally they do not survive to adulthood in these higher latitudes, gradually disappearing with the onset of winter (Beckley 1985). Many of these tropical species are the same species also being dispersed to temperate waters of south-eastern and south-western Australia (Beckley *et al.* 1987).

Tongues of the Agulhas Current can also be found off the lower west coast as isolated eddies entrapped in the cold north-flowing Benguela Current (Penrith 1976, Shannon & Agenbag 1987). However, any larvae originating from the tropical east coast carried by these eddies would be unlikely to settle given the unsuitable environment for reef fishes along the exposed sandy coasts of south-western Africa (Penrith 1976). Furthermore the cold conditions resulting from a combination of the Benguela Current and seasonal cold water upwelling would prevent survival.

Species of reef fishes originating from tropical west Africa are rare in south-west Africa, given the absence of a south-flowing current and the presence of large expanses of sandy coast between the Orange River (29°S) and southern Angola (17°S) (Penrith 1976).

South America

Little has been published on the dispersal of tropical reef fishes in temperate areas of South America. However, on the west coast, the combination of upwelling and the cold north-flowing Humboldt Current would obviously restrict the southward movement of tropical forms. Briggs (1974) indicated that the influence of these conditions has pushed the southern limit of the tropical fauna almost to the equator. On the eastern side, the warm Brazil Current flows almost as far south as the waters off the Rio de la Plata (35°S) where it meets the cold north-flowing Falkland Current. Briggs (1974) stated that the Brazil Current maintains a tropical fauna to at least Rio de Janeiro (23°S).

Therefore, it could be expected that the dispersal of tropical reef fishes by this current should continue well into the warm temperate regions of Brazil.

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